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Closely related invasive species may be controlled by the same demographic life stages

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Abstract

Invasive species that are closely related to each other may have similar population dynamics and, therefore, be controlled by targeting similar life stages. We studied two invasive knapweed species, spotted knapweed (*Centaurea stoebe* subsp. *micranthos*) and the hybrid meadow knapweed complex (*Centaurea* × *moncktonii*) in New York, USA, to determine their individual population growth rates (λ) across several sites over three years. Both knapweed species had growth rates that were greater than 1 (spotted knapweed λ ranged from 1.005–1.440; meadow knapweed λ ranged from 1.541–2.408), but there was high variability between years and sites. One study population of meadow knapweed was composed primarily of individuals of black knapweed ancestry (*C. nigra*), a species that, while introduced, is not invasive. For this population, the projected dynamics were stable (λ approximately 1). Elasticity analysis showed that the flowering-to-flowering stage contributed the most to population growth rate for six of seven sites and three additional transitions were also influential for four of seven sites of spotted and meadow knapweed: the seedling-to-vegetative stage, vegetative-to-flowering stage and flowering-to-seedling stage. We simulated how increasing vital rates would affect population growth and found that both spotted and meadow knapweed followed the same pattern. The vital rate of established seedlings maturing to flowering plants had the greatest effect on population growth, followed by the survival of new and established seedlings. In all cases, the responses were non-linear, with small initial changes having a large effect. Increases in the vital rates of later stages also tended to have a positive effect on growth rate, but the effects were more modest. Although the sensitivity analysis indicated that early vital rates had the largest effect on population growth, targeting these stages is not practical for management. Rather, reducing older life stage survival or delaying maturation of vegetative individuals would be more effective. The similarity between the population dynamics and how each life stage contributes to population growth provides support that protocols developed for one species should be effective for the other species with the caveat that any biological control agent should be directly tested on the target species before being utilised.

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Keywords
Biocontrol agents, biological invasions, *Centaurea* × *moncktonii*, *Centaurea nigra*, *Centaurea stoebe* subsp. *micranthos*, elasticity analysis, knapweed, population demography, population growth rate

Introduction

Invasive species have been increasing around the world and some of the worst invasive plant species invade agricultural fields and abandoned pastures (Müller-Schärer et al. 2018). The proliferation of invasive plant species into agricultural fields and meadows has caused economic damage and may require active management to remove or prevent further spread. Much of the focus on determining what makes species invasive has been on species traits such as plant height, seed size and growth rates (Westoby 1998; Drenovsky et al. 2012). Traits alone are often not sufficient to predict which species will become invasive (Catford et al. 2019); rather, invasiveness can be better predicted by the maximum population growth rate and how growth rate is altered by environmental conditions (Palma et al. 2021). However, far fewer studies examine population growth rate compared to those that measure traits thought to predict invasiveness, in part because data collection for demography studies is often more time consuming (Palma et al. 2021). To document population dynamics in invasive plants requires conducting a census of life history stages over several seasons to estimate the transitions between stages (i.e. growth and survivorship), as well as detailed measures of stage-specific fecundity (Milbrath et al. 2018). Variation in climatic conditions yearly can have large effects on the demographic transitions (Elderd and Doak 2006). Furthermore, invasive populations can experience very different demographic transitions at a local scale depending upon environment or habitat conditions, the land-use history of the area and the stage in the introduction history of the species, making it necessary to sample at multiple locations over several years to obtain meaningful estimates (Jongejans et al. 2010).

Uncovering the population dynamics of invasive populations through demographic studies has the additional benefit of providing information for control strategies that target specific life stages that contribute most to the population growth rate (Hansen and Wilson 2006). Detailed demographic data are critical for determining the demographic transitions between stages that have the greatest impact on population size so that these stages can be the target of population control efforts (Parker 2000). Determining the growth stages that will limit the population growth rate is also critical for matching invasive populations with potential biological control agents (Milbrath et al. 2018).

Matrix population models can be paired with detailed demographic data to estimate a population's projected growth rate (Caswell 2001). Detailed demographic studies may not be possible for most species, so determining whether closely-related species are regulated by the same demographic stage is helpful for determining management and control of populations. However, species with shared evolutionary histories and similar traits may undergo different population dynamics (Ramula et al. 2008) and

the contribution of each life stage to the population growth rate may also differ (Jelbert et al. 2019). Elasticity analysis provides a mechanism whereby one can examine how changes in one life stage affect population growth, while holding the other stages constant (Caswell 2001). Such studies allow for management to target the life history stages that will achieve the greatest reduction in population growth (Benton and Grant 1999). While average population growth rates can be useful for comparing amongst similar species and sites, year to year variability may make it challenging to predict projected population growth rates and, hence, management strategies (Akin-Fajiye and Gurevitch 2020). Year to year variability can be difficult to quantify in short term studies, but by having multiple plots in different sites, one can tease apart the larger climatic signal from the intra-site variation (Elderd and Doak 2006).

Knapweeds are an important genus of plant invaders that are short-lived perennials that grow abundantly in meadows and agricultural fields and include several species introduced to North America that have been classified as invasive (Coombs et al. 2004; Milbrath and Biazzo 2020). Spotted knapweed [*Centaurea stoebe* subsp. *micranthos* (Gugler) Hayek], originally from southeast and central Europe, has been present in the USA for over 100 years and spread throughout the eastern USA along disturbed ruderal habitats and railroad corridors (Broennimann et al. 2014; Akin-Fajiye and Gurevitch 2018). Meadow knapweed (*Centaurea* × *moncktonii* C.E. Britt.) has been increasing in the northeastern US (Milbrath and Biazzo 2020). Meadow knapweed originated as a hybrid between two other knapweed species, brown knapweed (*Centaurea jacea* L.) and black knapweed (*Centaurea nigra* L.) (Roché and Roché 1991). While both the parental species are introduced and sometimes classified as invasive, the hybrid species, meadow knapweed is more invasive than either of the parental species (Roché and Roché 1991). In this paper, we investigate whether spotted knapweed and meadow knapweed, two species with similar life histories and invasive behaviour, have similar projected population growth rates and whether the same life stages contribute to their population growth. Specifically, we ask:

1) What is the projected population growth of spotted knapweed and meadow knapweed and how variable are the growth rates between species, years and sites?
2) Which vital rates contribute the most to the population growth rates of each species and are the same vital rates important across species, years and sites?

Methods

Study species characteristics and invasion history

We measured vital rates in multiple populations of both spotted knapweed and meadow knapweed in western and eastern New York, USA. Both spotted and meadow knapweed are herbaceous short-lived perennial species with similar life histories. Spotted

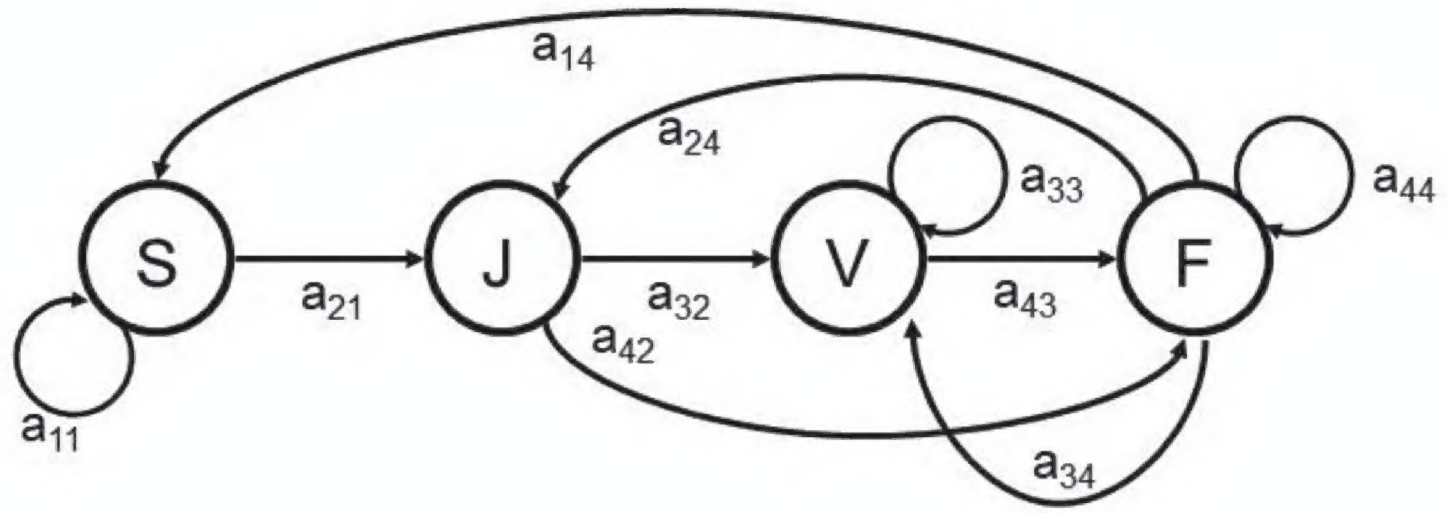
knapweed reproduces by seeds and plants typically flower in their second year; most flower every year thereafter (Emery and Gross 2005). Meadow knapweed reproduces by seeds and then the plants overwinter as a rosette of leaves; first flowering can take several years, but then plants usually flower annually thereafter (Roché and Roché 1991; Milbrath and Biazzo 2020).

Spotted knapweed is currently found in 46 U.S. States and six Canadian Provinces and was introduced from Europe in contaminated alfalfa (*Medicago sativa* L.) and soil ballast (Sheley et al. 1998). It has been a major rangeland and pasture weed in western North America and is an increasing problem in drier sites in eastern states including Arkansas, Michigan and New York (Winston et al. 2012; Carson and Landis 2014; Minteer et al. 2014; Akin-Fajiye and Gurevitch 2018). Meadow knapweed is found in 26 U.S. States and five Canadian Provinces (Keil and Ochsmann 2006; Poindexter et al. 2011; Winston et al. 2012) and is abundant in New York State and increasing in Vermont. Meadow knapweed is a fertile hybrid between black knapweed and brown knapweed (Hardy et al. 2000). Due to the hybrid nature of meadow knapweed and the variability in its traits, populations may consist of one, or both parental species plus the hybrid, creating a hybrid swarm (Lachmuth et al. 2019). Consequently, some putative meadow knapweed populations can contain substantial genetic contribution from one or both original parent species.

Data collection and analysis

We monitored three spotted knapweed populations in western New York, three putative meadow knapweed populations in west-central New York and one meadow knapweed population in eastern New York (Milbrath and Biazzo 2020; Suppl. material 1). The spotted knapweed populations grow on drier, well-drained soils, while the generally moist meadow knapweed sites were either abandoned pastures, grazed or still in active hay production (Milbrath and Biazzo 2020). The widely distributed fly *Urophora quadrifasciata* (Meigen) and the weevil *Larinus* sp. were present at all knapweed sites, which reduced the seeds present for both knapweed species to an unknown, but limited extent. Genetic identities of knapweed populations were verified through genomic analysis for meadow knapweed (Lachmuth et al. 2019), but not for spotted knapweed. After meadow knapweed populations were set up for monitoring, one of the sites (Jacobson) was identified as having predominantly genetic ancestry from black knapweed (*C. nigra*) (Lachmuth et al. 2019). Thus, our final population monitoring consisted of three spotted knapweed populations, three meadow knapweed populations and one putative predominantly black knapweed population (Suppl. material 1).

We designated four different life stages for monitoring and collection of demographic data: seeds in the soil seed bank (S), seedlings (J), vegetative plants (V) and flowering plants (F) (Fig. 1; Milbrath and Biazzo 2020). For purposes of the population modelling, 10 vital rates of germination, survival of life stages, transitions to other life stages and fecundity were primarily measured annually from August to the following August (usually before seed dispersal) for three transition years (2016–2019)



	S ($a_{.1}$)	J ($a_{.2}$)	V ($a_{.3}$)	F ($a_{.4}$)
S ($a_{1.}$)	$s_s(1-g)$	0	0	$fs_s(1-g)$
J ($a_{2.}$)	$s_s g s_{sj}$	0	0	fgs_{sj}
V ($a_{3.}$)	0	$s_{jv}(1-m_{jf})$	$s_v(1-m_{vf})$	$s_f r_{fv}$
F ($a_{4.}$)	0	$s_{jv} m_{jf}$	$s_v m_{vf}$	$s_f(1-r_{fv})$

Figure 1. Life-cycle diagram for the spotted and meadow knapweed populations and the associated population projection matrix. S = seeds in seed bank, J = seedlings, V = vegetative individuals, F = flowering plants. Arrows (a_{ij}) represent one-year transitions from August of year t to August of year t + 1 composed of vital rate combinations (shown in projection matrix; defined in Suppl. material 2). Matrix columns correspond with the stage ($a_{.j}$) from which individuals are transitioning at time t and rows indicate the stages ($a_{i.}$) to which individuals are transitioning at time t + 1.

(Fig. 1; Suppl. material 2). In total, ca. 42,000 seeds, 22,160 germinated seedlings and 7600 other life stages were marked and/or observed using a combination of germination trays and different-sized quadrats. Details of the population monitoring can be found in Milbrath and Biazzo (2020). We calculated vital rates for each developmental stage for each species and year at each site separately (Suppl. material 3).

Using the calculated vital rates, we derived transitions for all demographic stages by site for each year for each species (see transition matrix in Fig. 1). For example, flowering plants produced seeds (f), dispersed in late summer that, over the course of the next year, may remain dormant and enter the seed bank to increase the subpopulation of seeds, less any seed death (s_s) or reduction in seed numbers due to germination (1-g) that same year (transition a_{14}). A portion of other seeds may germinate to produce seedlings (g) although only a portion of those will survive to the following August (s_{sj}) to increase the subpopulation of seedlings (transition a_{24}). For each transition matrix, we projected the population growth rate (λ) at each site and year with starting values for each development stage at year 0 (2016). We also generated λ per site, based on the

average transitions of the three years of the study. For both sets of λ, we tested λ across all plots of each site for statistical differences from 1 (no change in population size) using Wilcoxon rank sum tests ($\alpha = 0.05$).

We also performed an elasticity analysis (Caswell 2001). For the elasticity analysis, we tested the sensitivity of λ for each species to proportional changes in vital rates. We computed λ for each transition matrix derived from varying values of each vital rate while retaining the other values at their mean values across years and sites. We changed the vital rates by 1% for 100 steps, except for flowering where we changed the number of seeds by intervals of 1000 seeds (Fig. 4). To determine how the transitions between developmental stages influenced λ, we averaged the transition matrices for each site and species and year to derive the elasticities for the transitions between development stages.

All computations were performed in R, in particular using the packages dplyr (Wickham et al. 2018) and reshape2 (Wickham 2017) for data organisation, ggplot2 (Wickham 2009) for visualisations, vegan (Oksanen et al. 2019) for permutation-based similarity tests and popbio (Stubben and Milligan 2007) for demographic analyses.

Results

The average population growth rate (λ) was significantly greater than 1 for two of the seven sites, indicating that these sites had expanding populations (Fig. 2). For the three spotted knapweed sites (Black Pond, McEnteer, Wehle), the average λ ranged from 1.005–1.440, while for the three meadow knapweed sites (FLNF or Finger Lakes

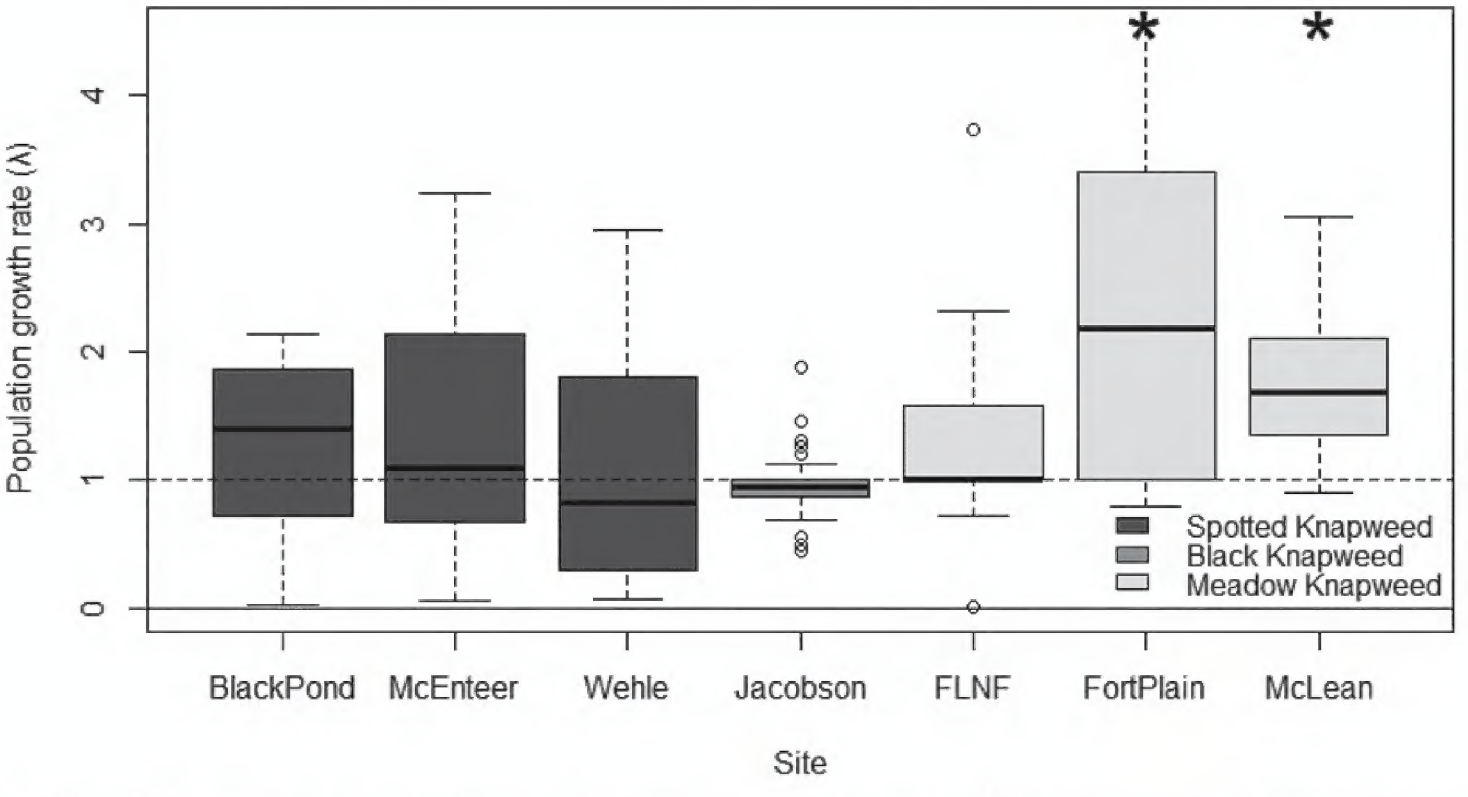


Figure 2. Population growth rate (λ) of knapweed species in each of the seven sites. Growth rates are based on the average transitions over three years. An asterisk shows population growth rates across all plots and years that were significantly greater than 1.0 ($P < 0.05$), with the dotted line indicating stable populations ($\lambda = 1$).

Table 1. λ and elasticities of λ for spotted knapweed, black knapweed and meadow knapweed, per location.

	Seed (S)	Seedling (J)	Vegetative (V)	Flower (F)	λ
Spotted Knapweed – BlackPond					
Seed	0.034	0	0	0	1.233
Seedling	0	0	0	**0.161**	
Vegetative	0	**0.161**	**0.173**	0.038	
Flower	0	0	**0.199**	**0.234**	
Spotted Knapweed – McEnteer					
Seed	0	0	0	0	1.440
Seedling	0	0	0	**0.220**	
Vegetative	0	**0.201**	0.102	0.087	
Flower	0	0.018	**0.288**	0.083	
Spotted Knapweed – Wehle					
Seed	0	0	0	0	1.005
Seedling	0	0	0	0.120	
Vegetative	0	0.099	0.014	0.007	
Flower	0	0.022	0.106	**0.632**	
Black Knapweed – Jacobson					
Seed	0	0	0	0	0.968
Seedling	0	0	0	0.048	
Vegetative	0	0.048	0.067	0.038	
Flower	0	0	0.086	**0.713**	
Meadow Knapweed – FLNF					
Seed	0	0	0	0	1.541
Seedling	0	0	0	0.079	
Vegetative	0	0.079	0.114	0.004	
Flower	0	0	0.082	**0.642**	
Meadow Knapweed – FortPlain					
Seed	0	0	0	0	2.408
Seedling	0	0	0	**0.203**	
Vegetative	0	**0.188**	0.030	0	
Flower	0	0.015	**0.189**	**0.375**	
Meadow Knapweed – McLean					
Seed	0	0	0	0.001	1.754
Seedling	0.001	0	0	**0.207**	
Vegetative	0	**0.208**	0.068	0.012	
Flower	0	0	**0.220**	**0.285**	

Bold numbers indicate highest elasticity values (> 0.15) for each population.

National Forest, Fort Plain, McLean), the average λ was higher, ranging from 1.541–2.408 (Table 1). In contrast, the Jacobson site with black knapweed genetic ancestry experienced a slight decrease in population growth, with the average λ being 0.968.

Average growth rates can obscure important variability that occurs between species at each site and year. For spotted knapweed, two sites (McEnteer and Wehle) showed similar patterns of population growth (Suppl. material 4, Fig. 3) characterised by λs below 1 in the first year, indicating declining populations. However, in year 2, the λs were significantly higher than 1 at both sites, indicating populations were growing. In Year 3, both sites had λs lower than 1 indicating populations were declining or stable; however, the results were not statistically different from 1, indicating uncertainty of the

Figure 3. Population growth rate (λ) of knapweed species in each of the seven sites per year. Growth rates are shown for an August to August transition for **a** 2016–2017 **b** 2017–2018; and **c** 2018–2019. An asterisk shows population growth rates across all plots significantly greater than 1.0 ($P < 0.05$), with the dotted line indicating stable populations ($\lambda = 1$).

population decline (Fig. 3). At the third site (Black Pond), λs were greater than 1 for years 1 and 2, but less than 1 for year 3, although none was statistically different from 1 (Fig. 3). This lack of significance reflects the high variance in the plot-based estimates.

For meadow knapweed populations, the three sites were different from each other in their population dynamics. At the McLean site, λ was significantly greater than 1 for all three years of the study (Fig. 3). At Fort Plain in year 1, λ did not differ from 1, but it was significantly greater than 1 in the two subsequent years. In particular, the population grew markedly in year 2 with an average λ of 3.191, followed by another year of high growth rates (average λ = 2.202) (Suppl. material 4). At the FLNF site, λ was not different from 1 during any of the three years of the study (Fig. 3). However, in year 1 and year 2, there was high variability in the estimated λs. Population growth rates at the Jacobson site with black knapweed ancestry hovered near 1 each year with low variation in the estimated growth rates (Fig. 3).

Elasticity analyses allow for a determination of how life stage transitions contribute to the population growth rate. For six of seven sites, the flowering-to-flowering stage (a_{44}) had the largest elasticity, contributing 23 to 71% to the population growth rate (Fig. 1, Table 1). The single exception was the McEnteer site where the flowering-to-flowering transition had little effect on the population growth rate. For three of these sites (spotted knapweed-Wehle, meadow knapweed-FLNF, putative black knapweed-Jacobson), the flowering-to-flowering transition contributed 63% or more to λ, while other transitions contributed little (Table 1). For the remaining four sites of both spotted and meadow knapweed, three additional transitions had roughly similar and large contributions to the population growth rate: seedling-to-vegetative stage, a_{32}; vegetative-to-flowering stage, a_{43}; and flowering-to-seedling stage, a_{24} (Fig. 1, Table 1). These three transitions each contributed between 16 to 29% to population growth rate and involved seven of the ten vital rates measured (Fig. 1, Suppl. material 2). An additional transition, the vegetative-to-vegetative stage (a_{33}), was only important for the spotted knapweed site of Black Pond (Table 1).

We simulated how a change in each vital rate would affect population growth (Fig. 4). Not surprisingly, one vital rate (reversion from the flowering stage to a vegetative stage, r_{fv}) showed a decline in λ with an increased proportion of reversion. The remaining vital rates showed a slight to substantial increase in λ with an increase in the vital rate (Fig. 4). Spotted knapweed and meadow knapweed showed similar patterns (curves) for most vital rates, except for new seedling survival (s_{sj}) and fecundity (f). In the latter two cases, spotted knapweed may be more sensitive to changes in seedling survival and fecundity than meadow knapweed as indicated by steeper and diverging curves (Fig. 4). The vital rate that had the largest effect on λ was the seedling-to-flowering maturation rate (m_{jf}), whereas three vital rates had relatively little effect on λ for spotted and meadow knapweed: seed survival (s_s), survival of flowering plants (s_f) and the flowering-to-vegetative stage transition (r_{fv}) (Fig. 4). The remaining six vital rates appeared to have similar effects on λ. Notably, the putative black knapweed population responded differently from the two other knapweed species (Fig. 4). For this population, a decrease in the survival of flowering plants and an increase in the flowering-to-vegetative stage may reduce λ below 1 (Fig. 4).

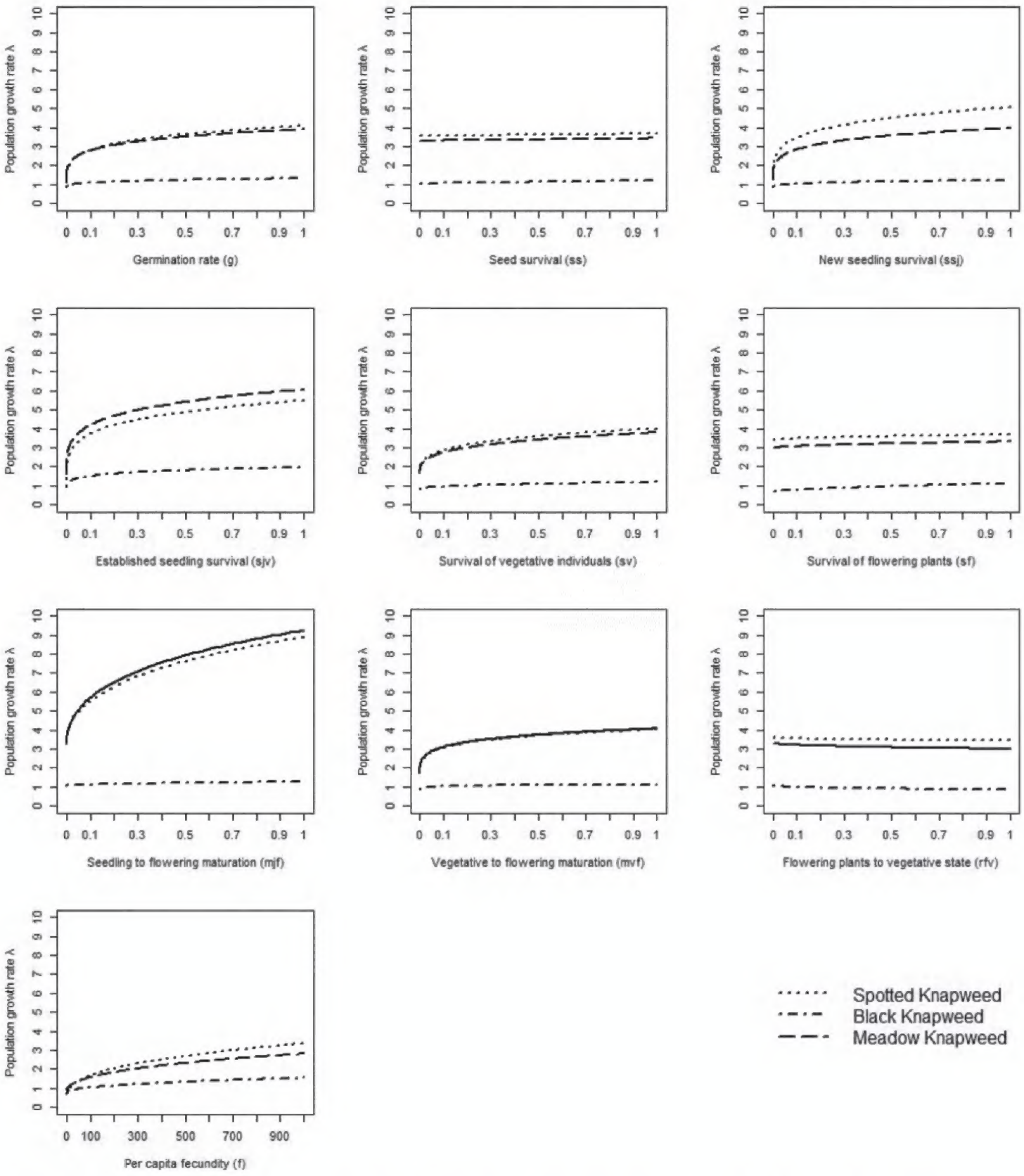


Figure 4. Sensitivity of each knapweed species' population growth rate to changes in specific vital rates.

Discussion

The increasing prevalence of spotted knapweed and meadow knapweed in the eastern USA makes understanding the population dynamics and the demographic transitions that contribute to their expansive growth rate important. Both spotted and meadow knapweed had average population growth rates (λ) greater than 1, indicating most of their populations are increasing in the Northeastern US and are capable of further spread and invasion. Although no similar studies on meadow knapweed exist, there are several studies that have projected the population growth of spotted knapweed (Emery

and Gross 2005; Maines et al 2013; Akin-Fajiye and Gurevitch 2020). In Michigan, Emery and Gross (2005) determined the average population growth was greater than 1 (1.17), but found variation amongst years with one year having a growth rate less than 1. Akin-Fajiye and Gurevitch (2020) determined population growth rates from experimental populations of spotted knapweed on Long Island, New York. In their study, the projected population growth of spotted knapweed ranged from 2.14 under high density and undisturbed conditions to 3.64 under low density conditions with disturbance. In our spotted knapweed populations, population density was high (Milbrath and Biazzo 2020) and, thus, the lower growth rates are consistent with Akin-Fajiye and Gurevitch (2020). Maines et al. (2013) projected population growth for spotted knapweed around Boulder, Colorado and found rates ranging from 1.3 to 1.7, with higher growth rates associated with higher precipitation.

As found in other studies (Emery and Gross 2005; Akin-Fajiye and Gurevitch 2020), we found large variation in λ amongst years. For spotted knapweed populations, two of the three populations appeared to alternate between low and high growth rates, a pattern consistent with a strong density-dependent response. This is consistent with the density-dependent response reported by Emery and Gross (2005) where lower growth rates were found with higher population densities. While density-dependence may play a role in the long-term dynamics of spotted knapweed, the short timeframe of our study makes it impossible to conclude that the populations were cycling between low and high densities. Moreover, environmental stochasticity and demographic stochasticity could also result in variable projected growth rates. For example, during our study, we observed a severe drought in 2016 that reduced spotted knapweed survival at the Wehle site. Similarly, a large population of *Larinus* weevils at the McEnteer site in 2018 was correlated with reduced seed production and subsequent low seedling recruitment (Milbrath and Biazzo 2020). However, the degree to which these and other unidentified factors are influencing specific populations is unclear.

For meadow knapweed, population growth rates were overall higher than for spotted knapweed (excluding the population composed primarily of black knapweed individuals). Both meadow knapweed and spotted knapweed populations showed overall high within-population variation in growth rates. Previous studies of the same meadow knapweed populations have shown high phenotypic variation in capitula traits (Lachmuth et al. 2019) and morphological traits (Molofsky, unpublished data). Genetic studies on the same population found that these meadow knapweed populations are advanced generation (beyond F2) recombinant hybrids and, thus, would be expected to express high levels of individual phenotypic variation (Lachmuth et al. 2019). The high phenotypic variance in hybrid meadow knapweed seems to result in a similarly high variance in vital rate parameters and projected population growth. Our previous genetic work also determined that one of our sites (Jacobson) had a high proportion of individuals with black knapweed genetic ancestry (Lachmuth et al. 2019). This site was projected to have an average population growth that is less than 1 with low variance across each site and across all years. This might suggest that populations composed of individuals with high amounts of black knapweed genetic ancestry may be declining; yet with just a single site with this ancestry background, this hypothesis must await

further investigation. Herbivory by slugs and snails was also high at this site (as well as other meadow knapweed sites); thus, subsequent mortality of earlier life stages undoubtedly influenced population growth, although to what degree is unknown (Milbrath and Biazzo 2020).

Projecting long-term invasive spread from short term studies should be done cautiously. This is especially true in the context of biological invasions, which are characterised by non-equilibrium population dynamics that often reflect the invasion history and the length of time since the species has colonised a given location (Ramula et al. 2008). A recently colonised site experiencing low density dependence may initially experience extremely high growth rates that may eventually become stabilised as the population ages and density dependence becomes more important (Ramula et al. 2008). In our study, knapweed populations had been present for several years prior to the study (Milbrath and Biazzo 2020). Thus, we expect the population dynamics estimated for these sites should reflect established populations. In fact, the relatively high density of plants within our sites indicates that some populations may have been limited by density (Milbrath and Biazzo 2020). While some populations showed average population growth rates greater than 1, there was also high spatial and temporal variability and, at any site and year, the growth rate could be stable or declining (Fig. 3). Moreover, it is not clear how much additional spread into adjacent sites is occurring. In knapweed species, the seeds are present in capitula, which drop to the ground. Thus, the seeds should be contained locally, with occasional longer distance seed dispersal through animal and human movement. This indicates that the risk of current populations spreading to new sites would be limited without large disturbance and human movement of seeds. However, the spread of meadow knapweed can come not only through spread of seeds to new sites, but also through the spread of their genes through pollination of either black knapweed or brown knapweed or through backcrossing with a hybrid meadow knapweed (Lachmuth et al. 2019). In the northeastern US where meadow knapweed has increased recently, its increase may be due to both hybridisation creating more meadow knapweed populations and their higher invasiveness compared to the two parental species.

The elasticity analysis allows us to predict how changes in individual life stage transitions will impact population growth. In the northeastern US, the most influential transition was the proportion of flowering plants that survived to flower in subsequent years. Thus, reducing population growth rates below 1 may be achieved by increasing mortality of adult plants. Management of other stages contributing to other influential transitions may also be productive in reducing population growth, i.e. the production of seed and subsequent recruitment of new seedlings into the population (via the flowering-to-seedling transition), the survival of established seedlings to the vegetative juvenile stage in their second year of growth (seedling-to-vegetative transition) and vegetative individuals flowering the following year (vegetative-to-flowering stage). The vegetative-to-flowering transition involved both the maturation of vegetative juvenile plants that had never previously flowered, as well as previously flowered individuals that became non-flowering for a year (Milbrath and Biazzo 2020). It was not always possible to distinguish these two sources, so they were combined in our analyses. These

results are comparable to Emery and Gross (2005) and Akin-Fajiye and Gurevitch (2020) for spotted knapweed although they used a five- and three-stage model, respectively, instead of the four-stage model that we used. We separated seedlings from vegetative individuals (unlike Akin-Fajiye and Gurevitch (2020)) because we could accurately track seedling fates, but we only included one flowering adult stage (as opposed to Emery and Gross (2005)) because the variation in stem number amongst sites and species in our study did not clearly indicate additional logical subdivisions to use. In another study of spotted knapweed carried out in Montana, Jacobs and Sheley (1998), using sensitivity analysis with a different demographic modelling approach, also identified survival of juvenile and adult plants, a juvenile-to-adult transition and seed production as important. Thus, vulnerable transitions seem to be consistent across spotted knapweed populations in different regions of the USA.

Reducing the rate of the four transitions, alone or in combination, should reduce population growth of northeastern populations of spotted and meadow knapweed by targeting the specific vital rates integral to these transitions (Fig. 1, Suppl. material 1). In their meta-analysis of invasive plants, Ramula et al. (2008) suggested that reductions in growth, fecundity or combinations of reductions including survival should result in declining populations in short-lived species like knapweeds. Based on our results, this could involve increasing mortality of flowering individuals (flowering-to-flowering transition), reducing fecundity directly and/or increasing mortality of newly-germinated seedlings (flowering-to-seedling transition), reducing the survival of established seedlings (seedling-to-vegetative transition) or reducing the survival of vegetative individuals and/or delaying or preventing the flowering of vegetative plants (vegetative-to-flowering stage). While the established seedling-to-flowering maturation rate had a large effect on λ (Fig. 4), it was rare or did not occur amongst our sampled populations (0–5% rate, Milbrath and Biazzo (2020)) and, thus, would not be a realistic focus for control. Although not having a large effect as the previously discussed vital rates, the transition from flowering individuals back to the vegetative state was associated with lowering population growth rates (Fig. 4). Across years and sites, 19–40% of flowering spotted knapweed plants naturally reverted to a vegetative state, whereas 2–10% of meadow knapweed plants did (Milbrath and Biazzo 2020). Thus, mowing or haying fields that contain spotted and meadow knapweed may slow their spread.

The population growth trajectory as a function of changes in one life history transition while holding the rest of the life stage transitions constant allows us to hypothesise how environmental or genetic changes may result in altered population growth. For control purposes, it provides information about how altering a key life stage should affect a population's projected growth rate. In our study, we were also interested in understanding whether closely-related species with similar life histories would follow similar patterns. For all species, increases in fecundity had a large effect on population growth rates and the increase was similar across species, although spotted knapweed may be more sensitive to changes in fecundity. Reducing fecundity through targeted removal of seed heads and seeds, either through mechanical measures or biological control agents, may help reduce population growth rates and spread, but not necessarily cause population declines amongst the knapweed species. Biocontrol by seed head-infesting

insects alone, such as tephritid flies (*Urophora* spp.) and weevils (*Larinus* spp.), had not reduced densities of western USA populations of spotted knapweed despite seed reductions greater than 90% (Story et al. 2008). In our study, the natural occurrence of both the fly *U. quadrifasciata* and *Larinus* weevils may have suppressed the populations to an unknown degree, underestimating the projected increase for both species in the Northeastern US. However, it is unclear what impact these biocontrol agents will ultimately have on knapweed populations in the Northeast; data on insect densities and their per capita impact are currently lacking for this region of the country. This is particularly true for meadow knapweed that has larger flower heads and produces twice as much seed per head as spotted knapweed (Woods et al. 2008; Milbrath and Biazzo 2020). Myers and Risley (2000), using a simulation approach for the related diffuse knapweed (*Centaurea diffusa* Lamarck), predicted that a biocontrol agent must be able to kill later life stages of knapweed plants due to population-level compensation to reduced fecundity and/or seedling recruitment (early seedling survival). Other agents that fulfil this criterion are credited with declining spotted knapweed populations in Montana, specifically the root-boring weevil *Cyphocleonus achates* Fahraeus (Story et al. 2006). Similarly, for Colorado populations of spotted knapweed, the projected population growth rate from a combination of seed-head and root-boring insects was approximately 1 (Maines et al. 2013). Thus, reducing seed output and young seedling survival alone is not considered a viable approach to managing knapweed populations.

For spotted knapweed and meadow knapweed, the transition from established seedlings to mature flowering plants had the greatest effect on population growth, followed by the survival of new and established seedlings. In all cases, the responses were non-linear, with small initial changes having a large effect. Increases in the vital rates of later stages also tended to have a positive effect on growth rate, but the effects were more modest. Although the sensitivity analysis indicated that early vital rates had the largest effect on population growth, targeting these stages is not practical for management. Reducing older seedling, vegetative juvenile and adult survival or delaying maturation of vegetative individuals could limit population growth. Removing plants by mechanical means, such as pulling or through applications of herbicides, can aid spotted knapweed suppression and restoration efforts (MacDonald et al. 2019), but can be inefficient, time consuming and expensive. An alternative approach may be to identify a biocontrol agent that interferes at these stages. For example, the reported success of *Larinus minutus* Gyllenhal in reducing populations of diffuse knapweed in western North America (Winston et al. 2012) is apparently due to adult weevil feeding damage in addition to the expected impact from larval destruction of seeds. High densities of adult weevils can kill juvenile and adult plants through their feeding on rosette leaves and bolting stems (Myers et al. 2009). Such effects from *Larinus* adults have not been reported for spotted knapweed, but they do highlight the importance of post-seedling mortality that can be caused by agents such as *C. achates* (Story et al. 2006). Therefore, successful agents of western populations of spotted knapweed should be considered for use in the Northeast. However, it is unclear whether insect-induced plant mortality is effective as experimental assessments have usually involved the presence of multiple agents attacking different parts of the plant (Story et al. 2006; Maines et al 2013).

Further, Maines et al. (2013) suggested that other measures in addition to biocontrol would be needed to achieve a negative population growth rate of spotted knapweed in some locations, for example, a combination of appropriately-timed mechanical or chemical removal of plants that do not interfere with existing biocontrol agents. Given the similarity in the dynamics between northeastern populations of spotted knapweed and meadow knapweed, a similar approach could be applied to meadow knapweed. Although a few biocontrol agents released for spotted and diffuse knapweed control have naturally infested meadow knapweed in the Northwestern and Northeastern US (Coombs et al. 2004; Woods et al. 2008), new biocontrol agents may be needed as current successful agents may not survive or develop in the moister habitats containing meadow knapweed, they may not easily transfer or may have a smaller impact. In contrast, for the site with black knapweed ancestry, altering vital rates had minimal effect on overall population growth rates with the one exception being the survival of flowering plants. The low number of single origin populations found for both black knapweed and brown knapweed in the Northeast suggests extinction by hybridisation for these two parental species. Thus, management efforts and biocontrol strategies should be focused exclusively on the spotted and meadow knapweed populations.

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Supplementary material 1

Knapweed locations in New York State. FLNF = Finger Lakes National Forest

Authors: Jane Molofsky, Dominik Thom, Stephen R. Keller, Lindsey R. Milbrath

Data type: Location of study sites (table)

Explanation note: Information on the location of each study site.

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Link: https://doi.org/10.3897/neobiota.82.95127.suppl1

Supplementary material 2

Lower-level vital rates for the knapweed matrix population model

Authors: Jane Molofsky, Dominik Thom, Stephen R. Keller, Lindsey R. Milbrath

Data type: table

Explanation note: Lower level vital rates used in the matrix population models.

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Link: https://doi.org/10.3897/neobiota.82.95127.suppl2

Supplementary material 3

Vital rates for each knapweed species by each site and by each year

Authors: Jane Molofsky, Dominik Thom, Stephen R. Keller, Lindsey R. Milbrath

Data type: table

Explanation note: Vital rates for spotted knapweed, black knapweed and meadow knapweed per site and year of measurement.

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Supplementary material 4

Elasticities by species by plot by site by year

Authors: Jane Molofsky, Dominik Thom, Stephen R. Keller, Lindsey R. Milbrath

Data type: table

Explanation note: λ and elasticities of λ for spotted knapweed, black knapweed and meadow knapweed per site and year of measurement.

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